# **Cnidae of Scleractinia**

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Abstract.—Corals and corallimorpharians are considered cnidarians with simple cnidae. This work shows that such a statement is relative, and depends upon the accuracy of the observation. The cnidae of tentacles and mesenterial filaments of 60 species belonging to 17 families of Scleractinia and three families of Corallimorpharia were studied using Normarski optics. The diversity of the cnidae (morphological patterns and their varieties) is described and illustrated, and their distributions are given: In addition, a new type of cnida from the mesenterial filaments of Agariciidae is recorded. Synonym lists of the names used by other authors for the cnidae of Scleractinia and Corallimorpharia are also included, and aspects of their terminology are discussed. Diversity in the cnidae of Scleractinia confirms the potential of soft tissues as an important source of characters that should be explored in taxonomic studies. When used with other characters, the descriptions of cnidae will contribute to the improvement of studies on coral taxonomy and systematics.

The knowledge of the cnidae in terms of their diversity, size and distribution, has been considered as a useful taxonomic character for many groups of Cnidaria (see Pires & Pitombo 1992). The nematocysts represent categories that are usually constant (Gravier-Bonnet 1987, Pires 1988) and their structural complexity provides many features for comparison (Tilbury & Cameron 1989). The systematics of the Scleractinia, the largest order of the subclass Hexacorallia (=Zoantharia) (Wells 1956), with approximately 225 recent genera and 1500 species (Cairns 1990), is not fully satisfactory (Chevalier & Beauvais 1987), being based primarily on skeletal morphology (Wells 1956).

One of the reasons for the neglect of coral cnidae studies is the lack preservation of their tissue. It is not routine in most scientific collections to preserve scleractinian coral tissues, especially in formalin, because the skeleton is the primary or only taxonomic source of characters. Problems with nematocyst nomenclature, some of which have been recently discussed by England (1991), have also made it difficult to understand and compare studies that have included data on cnidae.

The goal of this paper is to describe the diversity of cnidae occurring in tentacles and mesenterial filaments of Scleractinia and to propose a detailed terminology to classify subtypes of coral cnidae. This study is based on a large array of taxa and on features that can be observed through light microscopy, which is easily accessible to most researchers. To help in the understanding and interpretating other papers, synonym lists of terms used for cnidae by other researchers are included. The cnidae of the Corallimorpharia were also studied here due to their great similarities with the Scleractinia, as has been previously pointed out (Schmidt 1974, den Hartog 1980).

The cnidae are structures unique to the

Cnidaria and it seems clear that they must have a distinct place in phylogenetic speculations (Vervoort 1987). This paper contributes to explore some characteristics of coral cnidae, with the aim of providing new perspectives for systematics studies.

## Methods and Materials

The cnidae of tentacles and mesenterial filaments of Scleractinia were studied because these structures were found to have the most diversified cnidae (Pires, pers. obs.) Most observations were made on material fixed in 4% formalin and stored in 70% alcohol or 4% formalin. Some species from Brazil were maintained alive for examinating discharged cnidae. Decalcification of the skeleton was obtained using a solution of 10% formic acid and 5% formalin. Measurements were made with an eyepiece micrometer and illustrations were done using camera lucida. Preparations were examined with interference contrast, using a magnification of  $1250 \times$ . The synonyms of the cnidae are cited in the original publication language. For the evaluation of the diversity of the cnidae, the species listed below were examined. The taxa are listed in the same order used by Wells (1956) for Scleractinia (except Fungiacyathidae), and den Hartog (1980) for Corallimorpharia. The families are indicated in parentheses:

Scleractinia.—Suborder Astrocoeniina: Stephanocoenia michelinii (Astrocoeniidae); Madracis decactis (Pocilloporidae);

Suborder Fungiina: Agaricia agaricites, A. fragilis, Pavona sp., P. gigantea, Leptoseris cucullata (Agariciidae); Siderastrea stellata (Siderastreidae); Cycloseris marginata (?), Lithophyllum mokai, Fungia (Cycloseris) sinensis, Fungia (Verrillofungia) repanda, Fungia (Verrillofungia) concinna, Fungia (Fungia) fungites, Herpolitha limax, Polyphyllia talpina, Halomitra pileus, Zoopilus echinatus (Fungiidae); Leptopenus antarcticus (Micrabaciidae); Goniopora tenuidens, Porites astreoides (Poritidae); *Fungiacyathus* sp. (Fungiacyathidae);

Suborder Faviina: Favia gravida, F. leptophylla, Favites abdita, Platygyra daedalea, Colpophyllia natans, Cladocora debilis, C. arbuscula, Montastrea cavernosa (Faviidae); Astrangia rathbuni, Phyllangia americana (Rhizangiidae); Oculina patagonica, Madrepora sp. (Oculinidae); Meandrina braziliensis (Meandrinidae); Mussismilia hartti, M. braziliensis, M. hispida, Scolymia wellsi, Lobophyllia hemprichii, Lobophyllia sp. (Mussidae); Pectinia paeonia (Pectiniidae);

Suborder Caryophylliina: Caryophyllia ambrosia caribbeana, C. cornuformis, Deltocyathus italicus, D. calcar, D. eccentricus, Dasmosmilia lymani, D. variegata, Rhizosmilia maculata, Physogyra lichtensteini (Caryophylliidae); Flabellum sp., Javania cailleti (Flabellidae);

Suborder Dendrophylliina: *Balanophyllia europaea, Balanophyllia* sp., *Dendrophyllia* sp., (Dendrophylliidae).

Corallimorpharia.—Corynactis californica (Corallimorphidae), Ricordea florida (Ricordeidae), Discosoma carlgreni (Discosomatidae).

The studied material is deposited in the Collection of Cnidaria of the Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ) (Appendix), except *Pavona gigantea* (USNM 81542), *Pectinia paeonia* (USNM 90471) and *Madrepora* sp. from the National Museum of Natural History, Smithsonian Institution, Washington D. C.

## Results

The cnidae of tentacles and mesenterial filaments of the studied material can be grouped into five basic morphological patterns: spirocysts, holotrichs, b-rhabdoids, p-rhabdoids D (sensu Schmidt 1974) and agaricysts. Four of these cnidae were already well described in the literature (Weill 1934, Mariscal 1974, 1984; Schmidt 1974) and a new type is described (agaricysts). Table 1.—Diversity of cnidae and their varieties from tentacles and filaments of Scleractinia and Corallimorpharia.

### Spirocysts

Holotrichs

holotrich I [with one or two size classes] holotrich I (*Discosoma* var.) [close to holotrich I] holotrich II

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B-rhabdoids
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b-rhabdoid (1)
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b-rhabdoid (*Discosoma* var.) [close to b-rhabdoid (1)]

b-rhabdoid (*Favites* var.) [close to b-rhabdoid (1)] b-rhabdoid (2)

b-rhabdoid (Dendrophylliina var.) [close to b-rhabdoid (2)]

b-rhabdoid (3)

b-rhabdoid (*Physogyra* var.) [close to b-rhabdoid (3)]

P-rhabdoids D

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p-rhabdoid D(1)
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p-rhabdoid D(2) [with one or two size classes] p-rhabdoid D(3) p-rhabdoid D(4) p-rhabdoid D(5) p-rhabdoid D(6)

Agaricysts

However, subvarieties of previously described types (namely holotrichs, b-rhabdoids, and p-rhabdoids D) are herein introduced and characterized. Table 1 shows the types of cnidae here observed and their subvarieties. Table 2 shows the range of measurements of the cnidae observed. Tables 3–5 show main differences between subvarieties of holotrichs, b-rhabdoids, and p-rhabdoids D. Their distribution in different taxa of Scleractinia and Corallimorpharia is tabulated elsewhere (Pires & Castro, 1997).

# Spirocysts (Figs. 1A, 3A)

*Description.*—Capsule elongate and thinwalled, with a long tubule of uniform diameter, coiled in numerous spirals. Tubule without spines.

Remarks.—The spirocysts are especially

abundant in tentacles, although they may be seen in the other structures of the polyps of both Scleractinia and Corallimorpharia.

# Holotrichs

Description.—Capsule of varying shape and size (Table 2), from ellipsoid to very elongated cylinder. Tubule without differentiated parts - without the funnel-shaped "V" notch; long and helicoidal inside the capsule. Discharged tubule bears spines along almost all its length, arranged in distinct coils, and at right angles to the tubule surface.

*Remarks.*—Two morphological varieties of holotrichs were recognized in Coralli-morpharia and Scleractinia.

holotrich I (Figs. 1B, 2, 3B, 3C, Table 3)

- tangled cnidae (cnidae glomiferae) sensu Gosse 1860
- nematocyst type III sensu Matthai 1914
- nematocyst type IIIb and IIIc sensu Matthai 1928
- macrocniden sensu Seifert 1928
- haplonème isorhize holotriche sensu Weill 1934
- nematocyst B sensu Abe 1938
- holotrich sensu Carlgren 1940
- macrobasic p-mastigophore sensu Cutress 1955
- isorhize haploneme holotriche sensu Schmidt 1969
- haploneme holotriche I sensu Schmidt 1972
- haplonem holotrich I sensu Schmidt 1974
- haploneme holotrichous isorhiza sensu Mariscal 1974
- penicilli E sensu den Hartog 1980
- holotrichous isorhiza sensu Song 1988
- holotrich sensu England 1991
- holotrich I sensu Pires & Pitombo 1992

*Description.*—Capsule of varying shape and size (Table 2), from ellipsoid to very elongate cylinder; of rich contrast, with a very distinct tubule, usually arranged in many regular coils. Tubule isodiametric in dis-

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Fig. 1. Cnidae of tentacles of Scleractinia and Corallimorpharia, scale = 10  $\mu$ m. A, spirocyst of *Leptopenus* antarcticus; B, holotrich I of *Phyllangia americana*; C, holotrich I var. of *Discosoma carlgreni*; D, holotrich II of *Discosoma carlgreni*; E, b-rhabdoid (1) of *Fungia (Verrillofungia) concinna*; F, b-rhabdoid (1) of *Discosoma carlgreni*; G, b-rhabdoid (1) var. of *Favites abdita*; H, b-rhabdoid (2) of *Discosoma carlgreni*; I, b-rhabdoid (3) of *Stephanocoenia michelinii*; J, b-rhabdoid (3) var. of *Physogyra lichtensteini*; K, p-rhabdoid D(1) of *Montastrea cavernosa*; L, p-rhabdoid D(2) of *Fungia (Verrillofungia) concinna*; M, p-rhabdoid D(3) of *Siderastrea stellata*; N, p-rhabdoid D(6) of *Halomitra pileus*.

charged state, with spines of equal size present along whole length, except a small naked basal portion that often is present; latter portion easily seen in undischarged capsules (Figs. 1B, 2, 3B, 3C). Tubule of holotrich I of some Corallimorpharia presents an abruptly tapered and spineless distal tip.

Remarks.--Holotrichs I are sparingly pres-

Table 2.—Morphometrics of cnidae (except spirocysts) from tentacles and mesenterial filaments of Scleractinia and Corallimorpharia. All measurements are in  $\mu$ m. mcl = minimum capsule length; MCL = maximum capsule length; mcw = minimum capsule width; MCW = maximum capsule width; C = number of capsules measured; S = number of species in which the cnida was observed.

Cnidae	mcl	MCL	mcw	MCW	С	S	Fig
Tentacles							
holotrich I (1 size)	26.3	82.4	3.8	18.4	312	15	1B
holotrich I (2 sizes—small)	33.8	69.0	11.3	30.0	55	4	2
holotrich I (2 sizes—large)	51.3	145.0	21.3	60.0	73	4	2
holotrich I (Discosoma var.)	12.5	21.0	3.1	6.0	4	1	1C
holotrich II	21.9	42.0	5.0	12.0	20	1	1D
b-rhabdoid (1)	16.3	56.8	1.3	6.3	1074	44	1E
b-rhabdoid (Discosoma var.)	15.0	26.0	5.0	7.0	6	1	1 <b>F</b>
b-rhabdoid (Favites var.)	11.9	18.8	2.5	4.4	23	1	1G
b-rhabdoid (2)	7.5	11.3	1.3	2.5	10	1	1H
b-rhabdoid (3)	13.1	63.2	2.5	8.1	618	25	11
b-rhabdoid (Physogyra var.)	24.4	35.6	9.4	12.5	37	1	1J
p-rhabdoid D(1)	24.0	88.1	4.0	8.1	1144	32	1K
p-rhabdoid D(2)	20.0	67.5	3.8	13.1	641	21	1L
p-rhabdoid D(3)	10.6	25.0	3.1	7.0	139	6	1 M
p-rhabdoid D(6)	18.1	49.4	4.4	8.1	53	4	1N
Filaments							
holotrich I (1 size)	17.6	101.9	4.8	29.6	709	22	3B
holotrich I (2 sizes—small)	17.5	60.0	4.8	20.0	457	22	3C
holotrich I (2 sizes—large)	40.6	186.3	8.0	72.0	596	22	3C
holotrich II	8.1	29.4	2.0	12.5	497	14	3D
b-rhabdoid (1)	15.0	31.0	2.0	5.0	42	2	3E
b-rhabdoid (Favites var.)	13.8	29.4	3.1	5.0	22	1	3F
b-rhabdoid (2)	5.6	28.8	1.3	4.8	1038	49	3G
b-rhabdoid (Dendrophylliina var.)	11.3	16.3	3.1	4.4	38	1	3H
p-rhabdoid D(2) (1 size)	16.0	59.4	3.8	15.6	957	25	4A
p-rhabdoid D(2) (2 sizes—small)	16.9	77.6	4.0	11.9	666	25	4B
p-rhabdoid D(2) (2 sizes—large)	34.4	136.0	5.0	18.1	736	25	4B
p-rhabdoid D(3)	8.1	32.0	2.5	7.5	843	41	4C
p-rhabdoid D(4)	51.3	112.5	9.4	15.6	155	6	4D
p-rhabdoid D(5)	73.1	96.9	17.5	28.1	24	1	4E
Agaricyst	25.0	63.8	5.6	12.5	104	4	7

ent in the tentacles of corals. They occur in Micrabaciidae, Poritidae, Fungiacyathidae, Rhizangiidae, Oculinidae, in some Caryophylliidae (Caryophylliinae), Flabellidae and Dendrophylliidae, and are common in the tentacles of corallimorpharians. They occur in two size classes in the tentacles of Micrabaciidae, Flabellidae and Discosomatidae (Fig. 2). These size classes are present in both kinds of tentacles of Discosomatidae (marginal and discal), which uniquely presented also another distinct morphological variety of holotrich I. The latter shows poor contrast and is rather small (=holotrich I *Discosoma* var., Table 1, 2; Fig. 1C).

The occurrence of two distinct size classes of holotrich I is very common in the mesenterial filaments of some Faviina, Caryophylliina and Dendrophylliina (Fig. 3C). They also occur in two size classes in the mesenterial filaments of Corallimorpharia of the families Corallimorphidae and Discosomatidae. The anterior end of smaller ones is usually slightly tapered.





holotrich II (Figs. 1D, 3D, Table 3)

- haplonème anizorhize homotriche sensu Weill 1934
- haploneme holotrich II sensu Schmidt 1972 (part)
- homotrich sensu den Hartog 1980
- homotrich sensu England 1991

*Description.*—Capsule cylindrical, little refractive, of varying size (Table 2); content is composed of a long tubule, irregularly

coiled in small turns, filling whole undischarged capsule. Basal portion of tubule slightly enlarged and tapering toward distal end. Spines smaller than those of holotrichs I and shorter as the width of tubule decreases. Sometimes the slightly enlarged proximal part of tubule, which bears longer spines, is visible in undischarged capsule. When discharged, this portion is smaller than length of capsule.

Table 3.—Main differences between holotrichs I and holotrichs II.

Contras the cap	st of osule Capsule sizes	Discharged tubule	Undischarged tubule	Spines along discharged tubule	Spines in undischarged state
I high	n may occur in two distinct size classes	o isodiametric	regular coils, not filling the whole capsule	equal in size	clearly visi- ble
II low	only one size class	basal portion slightly en- larged	irregular coils, fill- ing the whole capsule	shorter as the tubule width decreases	undistinct

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Fig. 3. Cnidae of mesenterial filaments of Scleractinia, scale =  $10 \mu m$ . A, spirocyst of *Colpophyllia natans*; B, holotrich I (1 size class) of *Cycloseris marginata* (?); C, holotrich I (2 size classes) of *Phyllangia americana*; D, holotrich II of *Porites astreoides*; E, b-rhabdoid (1) of *Balanophyllia* sp.; F, b-rhabdoid (1) var. of *Favites abdita*; G, b-rhabdoid (2) of *Zoopilus echinatus*; H, b-rhabdoid Dendrophyllina var.

*Remarks.*—This cnida is very common in the mesenterial filaments of Poritidae, Faviidae, and Mussidae. It also occurs in the marginal tentacles of Discosomatidae.

## **B-rhabdoids**

Description.—Capsule of varying shape and size (Table 2). Tubule with no differentiated parts - without funnel-shaped "V" notch. Spines of proximal part of tubule slightly longer than those of distal portion. In the undischarged capsules, proximal part is visible as a rod. Tubule tapers very gradually; distal portion bears tiny spines.

Remarks.—Three morphological varie-

ties of b-rhabdoids were here recognized (b-rhabdoids (1), (2) and (3)).

b-rhabdoid (1) (Figs. 1E, 3E, Table 4)

- spirulae sensu Stephenson 1928
- basitriche sensu Weill 1934
- heteroneme b-rhabdoide sensu Schmidt 1969, 1972
- heteronem b-rhabdoid sensu Schmidt 1974
- basitrich sensu England 1991

Description.—Capsule cylindrical and elongated, sometimes slightly curved. Basal portion of tubule slightly enlarged, and can be seen in undischarged state as a thin axial

	Capsule contrast	Capsule shape	Size of enlarged basal portion of undischarged tubule	Arrangement of distal portion of undischarged tubule
(1)	high	elongated cylinder, sometimes slightly curved	almost equal to capsule length	few distinct regular coils
(2)	high	oval	approximately ½ of cap- sule length	few distinct regular coils
(3)	low	cylindrical	approximately 1/5 of capsule length	many small irregular coils, filling the whole interior of the capsule

Table 4.-Main differences of b-rhabdoids subvarieties.

rod, almost of same size of capsule length. Width of tubule diminishes toward distal end. Tubule arranged in few distinct regular coils, somewhat horizontally arranged inside capsule. When discharged, basal portion bearing larger spines is a little longer than entire length of capsule.

Remarks.—B-rhabdoid (1) is very common in the tentacles of most scleractinian families. They may also be present in the mesenterial filaments of Dendrophylliidae. A similar morphological variety of b-rhabdoid (1) was observed in the tentacles (Fig. G) and mesenterial filaments (Fig. 3F) of Favites abdita. That variety is more ellipsoid in shape, the tubule being longer and arranged in many coils. The coils fill all the interior of the capsule. The marginal and discal tentacles of Discosoma carlgreni contain another variety of b-rhabdoid, similar of b-rhabdoid (1). It is more translucent, the tubule is arranged in fewer coils, and usually the axial rod is oblique inside the capsule (Fig. 1F).

b-rhabdoid (2) (Figs. 1H, 3G, Table 4)

- mastigophore microbasique sensu Weill 1934
- microbasic b-mastigophore sensu Carlgren 1940
- b-rhabdoide sensu Schmidt 1969
- b-rhabdoid sensu Schmidt 1972, 1974
- spirulae 2 sensu den Hartog 1980
- microbasic b-mastigophore sensu England 1991

Description.—Capsule oval, very small

(Table 2), and of strong contrast. Basal part of tubule clearly distinguished in undischarged state, this rigid part approximately ½ of capsule length. Thinner part of tubule bears tiny spines; these latter arranged in few conspicuous turns. Thinner part of tubule often coiled down to rigid basal part.

*Remarks.*—B-rhabdoids (2) occur in the mesenterial filaments of all examined Scleractinia, and in some Corallimorpharia (Corallimorphidae), and exceptionally in the discal tentacles of Discosomatidae (Fig. 1H). A variety of b-rhabdoid (2) of larger capsule and shorter tubule occurs in the mesenterial filaments of Dendrophylliidae (Fig. 3H, Table 2).

b-rhabdoid (3) (Fig. 1I, Table 4)

- basitrichs sensu Weill 1934
- microbasic b-mastigophore sensu Carlgren 1940
- b-rhabdoide sensu Schmidt 1969, 1972
- b-rhabdoid sensu Schmidt 1974
- spirulae 1 sensu den Hartog 1980
- microbasic b-mastigophore sensu England 1991

*Description.*—Capsule of varying shape, but usually cylindrical, and slightly refractive. Proximal part of tubule bears spines somewhat longer than those from distal part. This region can be distinguished in undischarged capsule as a rod; approximately  $\frac{1}{5}$  of the length of the capsule; thicker than rods of b-rhabdoids (1) and (2). Distal part of tubule long; irregularly arranged; fills whole interior of undischarged capsule. Basal portion of tubule, approximately <sup>1</sup>/<sub>3</sub> of capsule length, in discharged state, with spines somewhat longer than those from thinner part of tubule.

*Remarks.*—This variety can be confused with holotrich II, especially in the undischarged state. Sometimes it is difficult to distinguish the slightly larger tubule basal portion, a characteristic of b-rhabdoids. Den Hartog (1980) considered them homologous, since he observed transitional stages between both types.

This variety occurs in the tentacles of Scleractinia (Astrocoeniidae, Pocilloporidae, Agariciidae, Fungiidae, Faviidae Montastreinae, Rhizangiidae, Oculinidae, few Caryophylliina, Dendrophylliidae) and Corallimorpharia (Ricordeidae and Corallimorphidae).

A morphological variety was observed in the tentacles of *Physogyra lichtensteini*. The proximal part of its tubule is exceptionally thick and very distinct (Fig. 1J)

P-rhabdoids D

- chambered cnidae (cnidae cameratae) sensu Gosse 1860
- type II sensu Matthai 1914, 1928
- hétéronème mastigophore microbasique sensu Weill 1934
- nematocyst A sensu Abe 1938
- microbasic p-mastigophore sensu Carlgren 1940
- p-rhabdoid D sensu Schmidt 1974
- penicilli D sensu den Hartog 1980
- microbasic p-mastigophore D sensu England 1991

Description.—Capsule of varying contrast, size and shape, from oval to very elongate cylinder. Tubule with two clearly differentiated parts: larger basal shaft and tapered distal tubule. These two regions delimited by sudden change in diameter of tubule and in length of spines; seen as funnelshaped "V" notch in undischarged capsules. Shaft often isodiametric; usually oriented straight inside capsule. In few cases it presents discrete coil in its base or, more rarely, shaft entirely coiled. This disposition of tubule varies inside capsule. Both regions, shaft and tubule, usually coarsely spined. When discharged, spines arranged at perpendicular to shaft surface; distinctly longer than shaft diameter. Tubule long; bearing spines rather smaller than those of shaft.

*Remarks.*—This cnida is exclusive to and very common in Scleractinia and Corallimorpharia. Six morphological varieties of p-rhabdoids D were here recognized (p-rhabdoids D(1), D(2), D(3), D(4), D(5) and D(6)).

p-rhabdoid D(1) (Fig. 1K, Table 5)

- nematocyst IIb sensu Matthai 1928
- penicilli D1 sensu den Hartog 1980
- microbasic p-mastigophores type III sensu Thomason & Brown 1986

Description.—Capsule elongate; cylindrical; slightly curved; of rich contrast. Shaft short (approximately <sup>1</sup>/<sub>3</sub> of capsule length) in undischarged state. A protruding tip commonly projects at anterior end of capsule. Spines of tubule clearly distinguished even in undischarged state.

*Remarks.*—This variety has a restricted distribution, occurring in the tentacles of most Scleractinia and commonly in the tentacles of Corallimorpharia, but not Discosomatidae.

p-rhabdoid D(2) (Figs. 1L, 4A, 4B, Table 5)

- nematocyst IId sensu Matthai 1928
- penicilli D3 sensu den Hartog 1980
- microbasic p-mastigophores type II sensu Thomason & Brown 1986

*Description.*—Capsule often cylindrical; of rich contrast. Spines of shaft arranged in obvious turns—approximately ½ of capsule length. Tubule long, irregularly arranged inside capsule.

Remarks.—This variety occurs in the

	Capsule contrast	Capsule shape	Length of undischarged shaft	Diameter of undischarged shaft	Spines in undischarged tubule
D(1)	high	elongated cylinder, slightly curved	approximately <sup>1</sup> / <sub>3</sub> of capsule length	isodiametric	clearly distinguish- able
D(2)	high	cylindrical	approximately ½ of capsule length	isodiametric	clearly distinguish- able
D(3)	low, almost transparent	cylindrical to oval	approximately ½ of capsule length	isodiametric	almost indistinct
D(4)	high	cylindrical	approximately equal to capsule length	isodiametric	clearly distinguish- able
D(5)	low	cylindrical	approximately equal to capsule length	anisodiametric with three distinct parts	clearly distinguish- able
D(6)	low	cylindrical	approximately 1/5 of capsule length	isodiametric	slightly distinguish- able

Table 5.—Main differences of p-rhabdoids D subvarieties.

mesenterial filaments of all Scleractinia and Corallimorpharia. In the mesenterial filaments of Astrocoeniidae and Pocilloporidae it is characteristically thick and clubshaped. It occurs in two distinct size classes in the mesenterial filaments of most Faviina (Fig. 4B). Exceptionally, it is also present in the tentacles of some Fungiidae (Fig. 1L).

p-rhabdoid D(3) (Figs. 1M, 4C, Table 5) - penicilli D2 [?] sensu den Hartog 1980

*Description.*—Capsule thin-walled; little refractive; almost transparent; often ovoid in shape. Shaft thin; approximately ½ of capsule length. Tubule short; occupying small portion of capsule. Spines of shaft and tubule almost indistinct in undischarged state.

*Remarks.*—This variety is very common in the mesenterial filaments of most Scleractinia and Corallimorpharia. It also occurs in the tentacles of Siderastreidae and Agariciidae.

p-rhabdoid D(4) (Fig. 4D, Table 5)

*Description.*—Capsule cylindrical; of rich contrast. Shaft long, in undischarged state filling almost whole capsule length; its basal portion slightly to coarsely coiled. Tu-

bule long; irregularly coiled. Spines clearly distinguished in both shaft and tubule.

*Remarks.*—This variety occurs in mesenterial filaments of some Fungiina and Caryophylliina. When present, it substitutes the larger class of D(2), which is common in the mesenterial filaments of some Faviina (Fig. 4B). Only undischarged capsules were observed. The length of the shaft of this variety is similar to those belonging to the "macrobasic state" of Weill (1934). The inclusion of this variety in p-rhabdoid D is tentative, pending the examination of discharged capsules.

p-rhabdoid D(5) (Fig. 4E, Table 5) - type IV sensu Abe 1938

Description.—Capsule very refractive in undischarged state. Shaft anisodiametric with three distinct parts: 1) short coiled basal portion, very thin and apparently naked, clearly distinguished in undischarged state; 2) middle part with abrupt enlargement, coiled, coarsely armed with long spines, and diminishes toward distal part, both in width of shaft and length of spines, comprises the longest and thickest part of shaft; and 3) distal part, gradually thicker, with very deep "funnel-shaped "V" notch. Tubule relatively short; irregularly coiled; with tiny spines.



Fig. 4. Cnidae of mesenterial filaments of Scleractinia, scale =  $10 \mu m$ . A, p-rhabdoid D(2) (1 size class) of *Madracis decactis*; B, p-rhabdoid D(2) (2 size classes) of *Favia leptophylla*; C, p-rhabdoid D(3) of *Cladocora debilis*; D, p-rhabdoid D(4) of *Polyphyllia talpina*; E, p-rhabdoid D(5) of *Goniopora tenuidens*.

*Remarks.*—This peculiar and very characteristic variety was found only in the mesenterial filaments of *Goniopora tenuidens*. Only undischarged capsules were examined. It clearly belongs to the "macrobasic state" of Weill (1934). The inclusion of this variety in p-rhabdoid D is tentative, pending the examination of discharged capsules. *Description.*—Capsule cylindrical; little refractive. Shaft thin; approximately  $\frac{1}{5}$  the capsule length. Spines of shaft and of tubule poorly distinguished in undischarged state. Tubule irregularly coiled; almost fills entire capsule.

*Remarks.*—Only undischarged capsules were examined. This variety can be confused with p-rhabdoids D(3); however, besides its larger capsule, it presents a proportionally shorter shaft, and the tubule is

p-rhabdoid D(6) (Fig. 1N, Table 5)

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Fig. 5. Agaricysts from the mesenterial filaments, scale =  $10 \mu m$ . A, discharged capsule and spineless tubule of *Agaricia agaricites*; B, discharging capsule and tubule with few attached and detached spines of *Agaricia agaricites*; C, undischarged capsule of *Pavona* sp.; D, undischarged capsule of *Leptoseris cucullata*.

somewhat longer than in p-rhabdoids D(3). It was only observed in the tentacles of species of *Fungia* and *Halomitra*.

# Agaricysts (Figs. 5, 6)

*Description.*—Capsule elongated; thickwalled; usually has a somewhat crushed appearance. Capsular content only slightly refractive. Tubule occupies almost whole length of capsule; arranged in two or three parallel bands (Fig. 5); running along longer axis of capsule. Apparently some spines are found around some of these bands (Figs. 5C, 5D). Discharged tubule long; anisodiametric (Fig. 5A). Proximal part of tubule approximately 2.4 mm in width, 4.0 mm in median region, and 1.6 mm close to tapering tip. Discharged tubule may seem to be spineless; however, spines can be observed on tubule surface without a distinct arrangement. Few unattached spines close to discharged tubule also present (Fig. 5B). Spines long; seem to loose contact with tubule when it discharges. Discharged tubule forms almost right angle with longer axis of capsule (Fig. 6).

*Remarks.*—This is a previously undescribed cnida, which was observed only in the mesenterial filaments of members of Agariciidae. Mariscal et al. (1977) classified the coelenterate cnidae in two major groups; helicoptychonemes and heteroptychonemes. The first group presents the un-



Fig. 6. Agaricyst from the mesenterial filaments of Agaricia agaricites, scale =  $10 \mu m$ . Discharged tubule forming almost a right angle with the longer axis of the capsule.

discharged thread helically folded to form multiple pleats in length and three pleats in circumference and includes the nematocysts and spirocysts. The second one have the undischarged thread not helically folded, with a variable number of pleats in circumference but none in length, and includes the ptychocysts. The agaricysts are similar to the heteroptychonemes described by Mariscal et al. (1977). Both present the uneverted tubule not helically arranged inside the capsule. When discharged, both tubules are anisodiametric, with longitudinal ridges along their length. Commonly, both tubules evert at an angle of about 60 to 90 degrees with the plane of the capsule.

## Discussion

A detailed study of the cnidae can provide characters for a better understanding of the different groups of Cnidaria. This holds true even among taxa in which cnidae have been previously considered of less taxonomic value. Even spirocysts, which show less structural variation, can be used as a source for comparative studies.

Weill's major work (1934) was a turning point in the study of nematocysts. However, its broad scope did not allow him to detail the cnidae of all cnidarian groups. In Scleractinia, for example, he superficially examined only eight species. He overlooked many cnidae, and he did not examine their distribution within the polyp. As the knowledge of the morphological structure of the cnidae of some groups accumulated, it became clear that some of Weill's categories included a wide variety of morphological types. The "rhabdoïdes" of Weill (1934), for example, represent a group of different types of nematocysts with few characteristics in common, and a most diverse structure. Schmidt (1974) divided the "rhabdoïdes" of Weill (1934) into four basic types: p-rhabdoids A, B, C and D. He subdivided these in some subcategories, and created a new terminology. Although his terminology is poorly known, his typology was accepted by some workers (den Hartog 1980, Östman 1983, England 1991, Pires & Pitombo 1992, Schlenz & Belém 1992). England (1991), pointed out the difficulties in using and adopting a codified alphanumeric system, without the descriptive elements of Weill's classification. Nevertheless, Schmidt's system is the one that most closely represents the diversity of the Anthozoa cnidae, and therefore is partially adopted in this paper.

According to Schmidt (1972, 1974) Scleractinia presents only one type of p-rhabdoid belonging to his category D. When discharged, the shaft of this type is rarely longer, frequently equal or shorter, than the length of the capsule (Schmidt 1972), corresponding to the microbasic state of Weill. However, the p-rhabdoids D(4) and D(5) cited in this paper, even when examined only undischarged, belong to the macrobasics of Weill, in contradiction to Schmidt's definition of his type D. Moreover, p-rhabdoids D present the same basic structure as p-rhabdoids A. Both of them have the length of the shaft and capsule ratio as described above. I believe the p-rhabdoids A and D belong to the same unit, as suggested by den Hartog (1980).

Problems in fitting cnidae into a previous system of classification led different authors to propose their own system (see synonymies here). However, some of these authors, and others who used these systems, did not always clearly define and illustrate the types they were working with. As a result, the usefulness of some papers on cnidae was partly lost. Misunderstandings related to the use of different terminologies must be avoided by using more precise descriptions and illustrations, based on large arrays of material.

Corals and corallimorpharians present the four basic morphological patterns of cnidae found in Hexacorallia, with the most diversified cnidae: spirocysts, holotrichs, band p-rhabdoids. Agaricysts were observed only in Agariciidae. In agaricysts, the arrangement of the undischarged tubule within the capsule and the appearance of the tubule following discharge look very similar to that of the heteroptychonemes described by Mariscal et al. (1977). The study of its ultrastructure in eletronic microscopy would be very helpful for describing it more precisely.

The evidence of the diversity occurring in the cnidae of Scleractinia presented in this paper support the important role of soft tissues as a source of useful taxonomic characters. The inclusion of morphological descriptions of cnidae in further studies will contribute to improving studies on coral taxonomy and systematics.

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## Appendix

Collection data of studied material from the Museu Nacional, Universidade Federal do Rio de Janeiro

(MNRJ). Donations of some specimens were obtained from the Instituto Oceanográfico, Universidade de São Paulo (IO/USP), through Dr. A. M. S. Vanin; from the Nationaal Natuurhistorisch Museum (Rijksmuseum van Natuurlijke Historie) (RMNH), through Dr. J. C. den Hartog; from the National Museum of Natural History, Smithsonian Institution (USNM), through Dr. S. D. Cairns; from the Bodega Marine Laboratory (BML) through Dr. C. Hand and from the Academia de Ciências de Cuba (ACC), through Dr. A. Herrera.

- *Agaricia agaricites* (Linnaeus, 1758). MNRJ 02686. Brazil, Bahia, Nova Viçosa, Coroa Vermelha Reef, coll. D. O. Pires 26 Jan 1991, det. D. O. Pires 3 Nov 1994.
- *Agaricia agaricites* (Linnaeus, 1758). MNRJ 02051. Brazil, Bahia, Prado, Coroa de Cumuruxatiba Reef, coll. C. B. Castro Jan 1992, det. D. O. Pires Jan 1992.
- *Agaricia agaricites* (Linnaeus, 1758). MNRJ 02052. Brazil, Bahia, Prado, Coroa de Cumuruxatiba Reef, coll. C. B. Castro Jan 1992, det. D. O. Pires Jan 1992.
- Agaricia agaricites (Linnaeus, 1758). MNRJ 02684.Brazil, Bahia, Abrolhos, SE Pedra Lixa, 16 m, coll.D. O. Pires 25 Jan 1991, det. D. O. Pires 3 Nov 1994.
- Agaricia agaricites (Linnaeus, 1758). MNRJ 02685.
  Brazil, Bahia, Abrolhos, SE Pedra Lixa, 16 m, coll.
  D. O. Pires 25 Jan 1991, det. D. O. Pires 3 Nov 1994.
- Agaricia fragilis Dana, 1848. MNRJ 02681. Brazil, Bahia, Prado, Aprofundados de Cumuruxatiba Reefs, coll. P. S. Young 30 Jan 1991, det. D. O. Pires 1 Nov 1994.
- Astrangia rathbuni Vaughan, 1906. MNRJ 02600. Brazil, Rio de Janeiro, Angra dos Reis, Queimada Pequena Island, coll. Coelenterology/MNRJ 6 Dec 1992, det. D. O. Pires 31 Aug 1994.
- Astrangia rathbuni Vaughan, 1906. MNRJ 01093. Brazil, Santa Catarina, Porto Belo, Quatro Ilhas Beach, coll. D. O. Pires 25 Jan 1986, det. D. O. Pires.
- Astrangia rathbuni Vaughan, 1906. MNRJ 02615. Brazil, Rio de Janeiro, Guanabara Bay, near "lage do Cação", coll. P. S. Young 19 Jun 1991, det. D. O. Pires 8 Sep 1994.
- Balanophyllia europaea (Risso, 1826). MNRJ 00090.
  Spain, Mediterranean, Cala Reona, Cabo Depalos, 1–2 m, coll. H. Zibrowius, 9 Apr 1981, det. H. Zibrowius. Obs.: donation RMNH.
- Balanophyllia sp. MNRJ 02377. Brazil, Bahia, Prado, Aprofundados de Cumuruxatiba Reefs. 17°00'S, 039°05'W, 18 m, coll. C. B. Castro 30 Jan 1991, det. S. D. Cairns. Obs.: donation USNM (USNM 90329).
- Caryophyllia ambrosia caribbeana Cairns, 1979. MNRJ 02376. Brazil, São Paulo, off Couves Island. 24°35.05'S, 044°12'W, 600 m, coll. R/V Prof. W.

Besnard 7 Dec 1988, det. P. S. Young & D. O. Pires 2 Mar 1994. Obs.: donation IO/USP.

- Caryophyllia cornuformis Pourtalès 1868. MNRJ 02442. Brazil, São Paulo, off Couves Island. 24°35.05'S, 044°12'W, 600 m, coll. R/V Prof. W. Besnard 7 Dec 1988, det. S. D. Cairns May 1991. Obs.: donation IO/USP.
- Cladocora arbuscula (Lesueur, 1821) MNRJ 02550. USA, off Florida, Gulf of Mexico. 25°45.53'N, 082°31.37'W coll. Continental Shelf Ass. MMS/ BLM 9 May 1983, det. S. D. Cairns. Obs.: donation USNM (USMN 71945).
- Cladocora debilis Milne Edwards & Maime, 1849. MNRJ 02407. Brazil, São Paulo, off Couves Island. 24°23.03'S, 044°18'W, 240 m, coll. R/V Prof. W. Besnard 8 Dec 1988, det. P. S. Young & D. O. Pires 7 Mar 1994. Obs.: donation IO/USP.
- Corynactis californica Carlgren, 1936. MNRJ 02130. USA, California, Bodega Harbor, coll. C. Hand, det. C. Hand. Obs.: donation BML.
- Corynactis sp. MNRJ 01453. Brazil, Rio de Janeiro, Rio de Janeiro, Cagarras Islands, 20.5 m, coll. C. C. Ratto 19 Nov 1988.
- (?) Cycloseris marginata (Boschma, 1923). MNRJ 02118. Indonesia, SW Sulawesi, coll. B. W. Hoeksema, 2 May 1985. Obs.: donation RMNH.
- Dasmosmilia lymani (Pourtalès, 1871). MNRJ 02372. Brazil, São Paulo, off Couves Islands. 24°25'S, 044°16.05'W, 320 m, coll. R/V Prof. W. Besnard 7 Dec 1988, det. P. S. Young & D. O. Pires 2 Mar 1994. Obs.: donation IO/USP.
- Dasmosmilia variegata (Pourtalès, 1871). MNRJ 02373. Brazil, São Paulo, off Couves Islands. 24°25'S, 044°16.05'W, 320 m, coll. R/V Prof. W. Besnard 7 Dec 1988, det. P. S. Young & D. O. Pires 2 Mar 1994. Obs.: donation IO/USP.
- Deltocyathus calcar Pourtalès, 1874. MNRJ 02378. Brazil, São Paulo, off São Sebastião Island. 24°42.05'S, 044°30'W, 320 m, coll. R/V Prof. W. Besnard 6 Dec 1988, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.
- Deltocyathus calcar Pourtalès, 1874. MNRJ 02380. Brazil, São Paulo, off Vitória Island. 24°31'S, 044°28'W, 240 m, coll. R/V Prof. W. Besnard 8 Dec 1988, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.
- Deltocyathus eccentricus Cairns, 1979. MNRJ 02409. Brazil, São Paulo, off Vitória Island. 24°41.01'S, 044°18.05'W, 510 m, coll. R/V Prof. W. Besnard 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.
- Deltocyathus eccentricus Cairns, 1979. MNRJ 02411. Brazil, São Paulo, off Couves Island. 24°35.05'S, 044°12'W, 600 m, coll. R/V Prof. W. Besnard 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.
- Deltocyathus italicus (Michellotti, 1838). MNRJ 02412. Brazil, São Paulo, off Vitória Island.

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24°41.01'S, 044°18.05'W, 510 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.

- Deltocyathus italicus (Michellotti, 1838). MNRJ 02413. Brazil, São Paulo, off Couves Island. 24°35.05'S, 044°12'W, 600 m, coll. R/V Prof. W. Besnard 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.
- Dendrophyllia sp. MNRJ 02352. Cabo Verde, S coast of São Tiago, SE Porto. 14°55'N, 023°30'W, 15 m, coll. 5 Jun 1982. Obs.: CANCAP VI 1982, Sta. 6 DO1 "Tydan", donation RMNH.
- Discosoma carlgreni (Watzl, 1922). MNRJ 00331. Brazil, Espírito Santo, Guarapari, Três Ilhas Archipelago, coll. S. Rosso et al. 17 Jul 1981, det. E. Schlenz & M. J. C. Belém 15 Oct 1981.
- Discosoma carlgreni (Watzl, 1922). MNRJ 02259. Brazil, Bahia, Abrolhos Archipelago, coll. F. B. Pitombo 23 Nov 1993, det. S. M. Pinto 8 Dec 1993.
- Favia leptophylla Verrill, 1868. MNRJ 02280. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. D. O. Pires et al. 24 Jan 1991, det. D. O. Pires 29 Dec 1993.
- Favia leptophylla Verrill, 1868. MNRJ 02574. Brazil, Bahia, Abrolhos, SE Pedra Lixa Reef, coll. Coelenterology/MNRJ 25 Jan 1991, det. D. O. Pires 26 Aug 1994.
- Favites abdita (Ellis & Solander, 1786). MNRJ 02342.
  Australia, Queensland, Swain Reefs Complex, Sweetlip Reef, 3–5 m, coll. P. Alderslade 4 Jul 1981, det. F. B. Pitombo 25 Jan 1981 Obs.: donation RMNH.
- Flabellum sp. MNRJ 02720. Off Guiana. 07°56'N, 057°12'W, 618 m, coll. "Luymes" Guyana Shelf Expedition 1 Sep 1970. Obs.: donation RMNH.
- Fungia (Cycloseris) sinensis Milne Edwards & Haime, 1851. MNRJ 02116. Indonesia, SW Sulames, coll.
  B. W. Hoeksena, 2 May 1985, det. B. W. Hoeksema 2 May 1985. Obs.: donation RMNH.
- Fungia (Fungia) fungites (Linnaeus, 1758). MNRJ 02679. Indonesia, S Sulawesi, N side of Samalona, 2–5 m, coll H. Moll 20 Nov 1980. Obs.: donation RMNH.
- Fungia (Verrillofungia) repanda Dana, 1846. MNRJ 02120. Indonesia, S Sulawesi, N side of Samalona, coll. H. Moll, 20 Nov 1980, det. H. Moll, 20 Nov 1980. Obs.: donation RMNH.
- Fungia (Verrillofungia) concinna (Verrill, 1864).
  MNRJ 02113. Indonesia, reef S. of Pilau Tikus, NW
  Java, coll. B. W. Hoeksema, 7 May 1983, det. B. W.
  Hoeksema, 7 May 1983. Obs.: conation RMNH.
- Fungiacyathus sp. MNRJ 02391. Brazil, São Paulo, off Vitória Island. 24°31'S, 044°28'W, 250 m, coll. R/V Prof. W. Besnard 8 Dec 1988. Obs: donation IO/USP.
- *Fungiacyathus* sp. MNRJ 02393. Brazil, São Paulo, off Ilha de São Sebastião, 320 m, coll. R/V *Prof. W. Besnard* 6 Dec 1988. Obs.: donation IO/USP.

- Goniopora tenuidens (Quelch, 1886). MNRJ 02459. Australia, Queensland, Swain Reefs Complex, Sweetlip Reef, 3–5 m, coll. P. Alderslade 4 Jul 1981, det. D. O. Pires May 1994. Obs.: donation RMNH.
- Halomitra pileus (Linnaeus, 1758). MNRJ 02119. Indonesia, North of Pulau Tikus, NW Java, coll. B.W. Hoeksema 11 May 1983, det. B. W. Hoeksema 11 May 1983. Obs.: donation RMNH.
- Herpolitha limax Esper, 1797. MNRJ 02115. Indonesia, W of Pulau Tikus, NW Java, coll. B. W. Hoeksema 10 May 1985, det. B. W. Hoeksema, 10 May 1985. Obs.: donation RMNH.
- Herpolitha limax Esper, 1797. MNRJ 02111. Indonesia, N side of Pulau Pajung, coll. B. W. Hoeksema 12 May 1983, det. B. W. Hoeksema 12 May 1983. Obs.: donation RMNH.
- Javania cailleti (Duchassaing & Michelotti, 1864).
  MNRJ 02383. Brazil, São Paulo, off São Sebastião Island. 24°35.04'S, 044°33.03'W, 184 m, coll. R/V Prof. W. Besnard 6 Dec 1988, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.
- Javania cailleti (Duchassaing & Michelotti, 1864). MNRJ 02384. Brazil, São Paulo, off Vitória Island. 24°23.02'S, 044°24.08'W, 180 m, coll. R/V Prof. W. Besnard 20 Jul 1987, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.
- Leptopenus antarcticus Cairns, 1989. MNRJ 02554. Antarctica, Ross Sea, approx. 200 Km W of Pennel Bank. 74°55'S, 174°12'W, 2022–2060 m, coll. R/V Eltanin, Usarp 7 Feb 1988, det. S. D. Cairns. Obs.: donation USNM (USNM 47482, 2 paratypes).
- Leptoseris cucullata (Ellis & Solander, 1786). MNRJ 02561. Venezuela, Curaçao, Isle Bay, 20 m, coll. R. P. M. BAK. Obs.: donation P. S. Young (MNRJ).
- Lithophyllum mokai Hoeksema, 1989 MNRJ 02114. Indonesia, SW Sulawesi, coll. B. W. Hoeksema 2 May 1985. Obs.: donation RMNH.
- Lobophyllia hemprichii (Ehrenberg 1834). MNRJ 02129. Seychelles, Alphonse Atoll, SE of the lagoon. 07°02'S, 052°44'E, 0–8 m, coll. R/V *Tyro* Seychelles Expedition 4 Jan 1993, det. J. C. den Hartog. Obs.: Netherlands Indian Ocean Expedition, donation RMNH.
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Physogyra lichtensteini Milne Edwards & Haime,

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